SEASONAL VARIATION AND DISTRIBUTION OF ZOOPLANKTON IN THE DEGLACIATING FJORD OF GLACIER BAY NATIONAL PARK, ALASKA

By

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Abstract

Seasonal composition and abundance of zooplankton along with their physical and chemical environment were investigated in Glacier Bay, AK. Collections were taken six times annually during 2016 and 2017 and separated into upper (0-50 m) and lower water column (50-180 m) strata. We found ~70 zooplankton taxa, with copepods dominating both abundance and biomass. We find that zooplankton concentrations within the bay are often an order of magnitude higher than outside. Zooplankton had species-specific preference for particular habitats, with significant populations of *Acartia* and *Oithona* in the upper column, *Metridia* in the lower column, and *Pseudocalanus* throughout the water column. Seasonality was clearly evident in the upper column, but less so at depth. Copepod nauplii had highest abundances during the spring, concurrent with the spring phytoplankton bloom. Total zooplankton were highest in the summer but with somewhat different timing between the two years. Highest annual zooplankton abundances were observed during May and July of 2016, while during 2017 the highest observed abundances shifted to July and September. These temporal shifts may be temperature-related as 2016 was generally warmer than 2017 by 1-2 °C. Community composition in Glacier Bay differs slightly in leading species from that of the Gulf of Alaska and adjoining Icy Strait. We suggest bathymetry in the bay is too shallow for *Neocalanus* and *Calanus* species to form overwintering populations.

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Introduction

Zooplankton are important to the flow of energy through marine ecosystems from primary producers to higher trophic levels. Despite the high abundance of planktivorous seabirds and marine mammals in many high latitude glacial fjords, their zooplankton prey communities are poorly described. In recent decades, several North Atlantic Arctic fjords in the Svalbard archipelago (Willis *et al.,* 2006; Basedow *et al.,* 2004), Norway (Skreslet *et al.*, 2015), and Greenland (Arendt *et al.*, 2016) have become better studied; however, zooplankton studies in North Pacific fjords are still limited and often inconsistent. Glacier Bay, for example, has had over a quarter-century of consistent oceanographic data monitoring (Danielson 2012), but zooplankton studies were sporadic, often only at glacial sites and during spring and summer months (Robards *et al.*, 2003). A notable exception is Prince William Sound (PWS), AK that has been included in several large research programs since the 1990s (e.g. Cooney *et al.,* 2009; Coyle and Pinchuk 2003; McKinstry and Campbell, 2018). Other fjords have seen sporadic attention (e.g., Auke Bay, AK), and often only to assess prey directly associated with upper trophic foraging aggregations (Coyle and Paul, 1992).

The Southeast Alaskan fjord of Glacier Bay is a geologically-young system. It has experienced rapid deglaciation over the last 235 years, and now stretches over 100 km from the mouth of the bay to its glacial termini (Etherington *et al.,* 2007). Despite rapid changes, Glacier Bay is thriving with marine life. Renowned as a pristine Alaskan fjord with high diversity and abundance of seabirds and marine mammals, this unique system hosts several species in threatened and endangered status. Species such as humpback whales, Stellar sea lions, spectacled eider, some murrelets, and Sockeye salmon utilize this fjord system for breeding, overwintering, feeding, or nursery areas (Robards *et al.*, 2003; Etherington *et al.*, 2007). Glacier Bay also

attracts nearly a half-million visitors each year. With iconic marine consumers so prominent in the reserve, and Glacier Bay likely at risk to change in future decades, understanding the bay's lower trophic productivity that supports the upper trophic productivity is a crucial need. To date, zooplankton studies in Glacier Bay are reported mostly in grey literature (Simenstad and Powell, 1990; Robards *et al.*, 2003). These only targeted select glacial sites with relatively coarse (~333 and 500 μm) mesh net sizes, providing a biased and incomplete characterization of the bay's ecosystem. Thus, the full extent and species-specific influence that zooplankton may have on upper trophic levels remain largely unknown in Glacier Bay (Renner *et al.,* 2012; Reisdorph and Mathis, 2014; Robards *et al.*, 2003).

This study seeks to develop a more comprehensive understanding of zooplankton populations throughout the Glacier Bay ecosystem. We asked how zooplankton community structure compares to that of nearby inland passages (i.e., Icy Strait) and the broader coastal Gulf of Alaska (GoA). In general, these coastal communities are comprised by a mixture of oceanic and neritic copepods, but with significant contributions by additional taxa such as larvaceans, euphausiids, amphipods, cheatognaths, and hydrozoan medusae (Coyle and Pinchuk, 2003; Coyle and Pinchuk, 2005). Additionally, meroplankton such as bivalve, barnacle, and echinoderm larvae can make significant numerical contributions to these communities seasonally (Kendall and Nakatani, 1991; Incze *et al.* 1996; Skreslet *et al.* 2015; Gluchowska *et al.* 2016; Sousa *et al.* 2016). The Icy Strait zooplankton community is dominated by copepods, but with somewhat shifted prominence of species compared to the Gulf (Park *et al.,* 2004). Early surveys collecting zooplankton at select sites in Glacier Bay indicated euphausiids, cheatognaths, and copepods to be prominent within their zooplankton community (Krieger and Wing, 1986; Simenstad and Powell, 1990). Given the isolation provided by the shallow (i.e., ~25-50 m) sill

across the Bay's mouth, and the considerable glacial melt that influences temperature and salinity dynamics, there are likely to be community differences from outside waters and even variations present throughout Glacier Bay, particularly near the glacier termini. The major objectives of this study include: 1) defining the seasonal variations in species composition, abundance and biomass, 2) describing the associations of co-occurring species of zooplankton, and 3) relating species composition to environmental parameters.

Study site

Glacier Bay is a 100 km long fjord in Southeast Alaska, carved out by retreating glaciers. Bathymetry varies between a shallow bay entrance (~25-50 m) to depths of up to 450 m between sills (Pickard, 1967). Deep water exchange occurs primarily in winter months (between December to February) from Icy Strait and Gulf of Alaska sources (Matthews, 1981). Turbulent mixing caused by bottom friction and breaking internal waves has been hypothesized important for mixing surface and subsurface waters, along with wind-induced mixing in the near-surface. Estuarine circulation can change in response to iceberg meltwater and their locations; generally, icebergs are trapped in the bay behind shallower sills in the upper inlets. As the

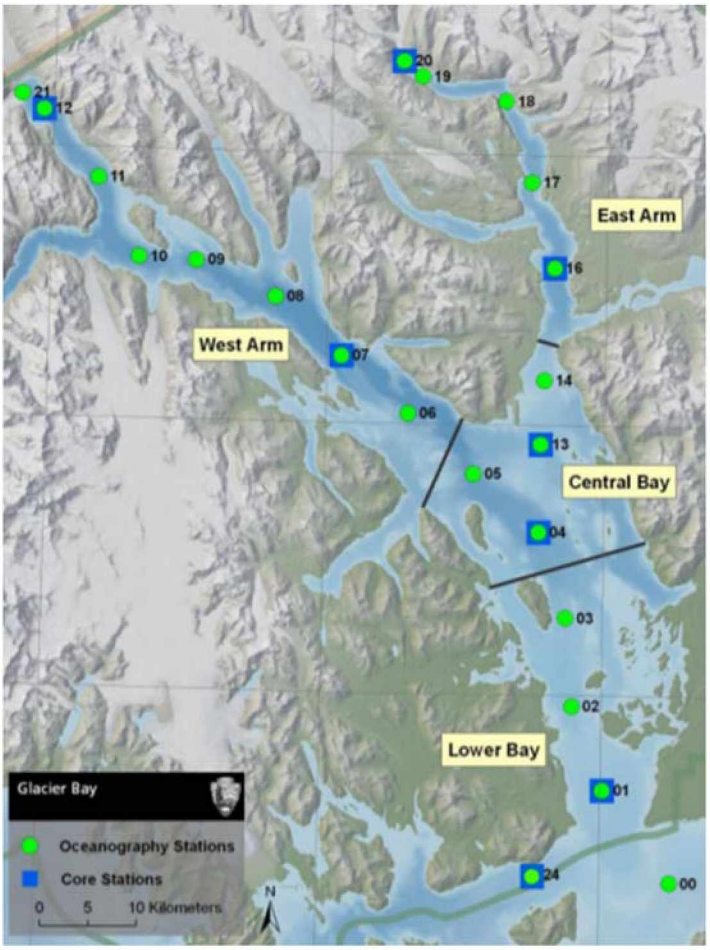

Figure 1. Station locations within Glacier Bay, Alaska, and its major domains: Lower Bay, Central Bay, West Arm, and East Arm

glaciers recede, the tidal prism expands, and the glacially impacted volume within the fjord increases, which in-turn increases the strength of tide-induced mixing (Matthews, 1981).

Climate in Glacier Bay is predominantly influenced by the Aleutian Low atmospheric pressure system in the Northern Gulf of Alaska from November to April, which delivers high precipitation rates and moderates winter temperatures. A weaker North Pacific high pressure system governs the greater Gulf of Alaska from May to October that reduces precipitation (Etherington *et al.*, 2007; Danielson, 2012). Glacier Bay has high rates of sedimentation and freshwater inflow due to wet and moderate temperatures that drive freeze-thaw cycles within the glaciers and surrounding mountain snowpack, contributing to numerous streams feeding into the bay (Etherington *et al.*, 2007; Danielson, 2012). Local weather variations occur from the strong katabatic winds that rush down the ice fields, glaciers, and mountains (Matthews, 1981).

Materials and Methods

Physical, chemical, and biological data was collected along mid-channel transects, spanning from the lower bay's entrance into Icy Strait (Station 24) and splitting into each major arm of the bay ending at each of the two glacial termini: Station 12 in Tarr Inlet, and Station 20 in Muir Inlet (Figure 1). Observations were collected over two years (2016-2017), building upon seasonal oceanographic monitoring conducted since the early 1990s (Pickard, 1967; Matthews, 1981; Robards *et al.*, 2003; Etherington *et al.*, 2007; Danielson, 2012). This project added water chemistry, phytoplankton biomass, and mesozooplankton collections to the continued observations of physical data. At each station, a Seabird 19+ V2 CTD (Conductivity Temperature Depth) recorded temperature, salinity, PAR (photosynthetically active radiation), and oxygen data from the surface to ~10 m from bottom. It was attached to a Seabird Eco-55 six-

bottle rosette system pre-programmed for bottle closures at maximum depth (~10 m above seafloor), ~100 m, 50 m, 30 m, 10 m, and 2 m from the surface. Water drawn from the rosette bottles was used for analysis of chlorophyll and macronutrients (nitrate, phosphate, and silicic acid). Seawater samples for macronutrient analysis were filtered (0.45 µm Whatman OE67) and frozen prior to analysis. Analysis was conducted on thawed samples using wet chemistry by labs conforming to WOCE standard (Gordon, 1993). Seawater samples (250 mL) for chlorophyll-a analysis were filtered at low pressure through Whatman GF/F filters. Filters were frozen until analysis using a Turner Trilogy fluorometer (Parsons *et al.,* 1984). Chlorophyll concentrations were integrated over the upper 50 m, and expressed as the average over that depth interval.

Zooplankton were collected with sequential vertical casts of a flow-metered 35 cm diameter 150 µm mesh Bongo net, separating the upper 50 m and lower water column (to near bottom or a maximum of 180 m) by using a General Oceanics double-trip mechanism. Contents from one side of each haul were preserved immediately in 10% buffered formalin, and the other in 95% ethanol. In the lab, formalin-preserved samples were subsampled using a Folsom splitter until they contained ~100 individuals of the most abundant taxa. Between 400-600 individuals were analyzed under the microscope by inspecting increasingly larger fractions of the sample for less abundant, larger-bodied taxa. Individual organisms were counted, measured, and classified to genus or species and stage of development, using the ZoopBiom software (Roff and Hopcroft, 1986). Weights were predicted using species-specific length-weight relationships (Questel *et al.,* 2013). The ZoopBiom program calculated abundance and biomass of each sample per unit volume. Samples preserved in ethanol were used for pteropod shell condition analyses, a different aspect of this project reported elsewhere.

Statistical Analyses

Abundance and biomass matrices were analyzed separately after fourth-root transformation (148 samples x 69 taxonomic categories). Species included in statistical analysis were observed at least three times in separate samples. A Bray-Curtis similarity index was used to determine zooplankton community similarity (Bray and Curtis, 1957), community structural divergence was investigated with non-parametric multi-dimensional scaling (nMDS), and hierarchical clustering routines in Primer 6 (Clarke and Warwick, 2010). Abundance and biomass data were analyzed within the entire water column, as well as separate upper and lower strata. We calculated mean temperature, salinity, and oxygen at each station for two depth intervals (upper stratum 0-50 m; lower stratum 50 m to bottom). Environmental parameters were related to zooplankton community structure using Primer's BEST routine.

Results

Physical and chemical environment

Annual cycles of temperature include a warming of surface temperatures during months of maximum light intensity (May through August), with warmest waters generally in the near-surface (e.g., 20 meters depth) (Figure 2). At the start of the year, in winter months, the lower water column (200-300 m) is slightly warmer than the surface (by ~0.5 °C) and generally weakly stratified. The water column typically has its lowest temperatures during March and April. Bay waters warm and freshen proceeding into spring and summer, particularly near the surface. By October, the surface temperatures begin to cool and mix downwards.

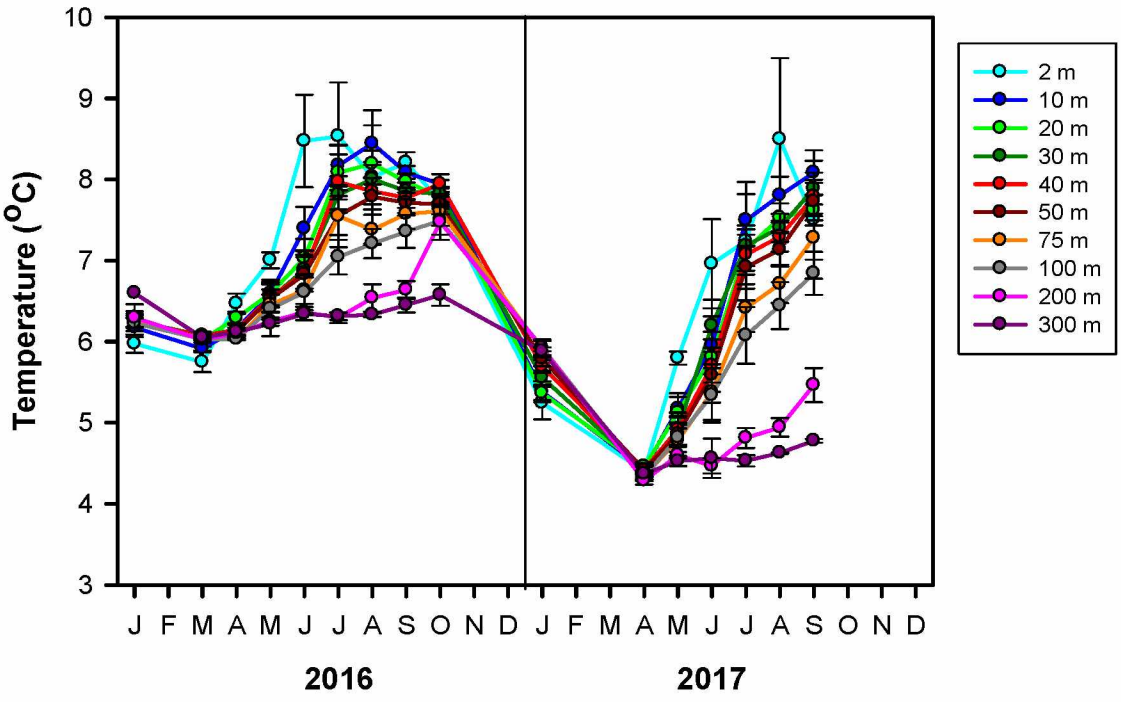

Figure 2. Mean temperatures for selected depths at core oceanographic stations in Glacier Bay shown in Figure 1. Standard error bars indicated in black.

Temperatures were generally 1.5-2 °C lower during 2017 relative to 2016. In both years, surface temperatures peaked during summer (~7.5-8.5 °C), while deeper waters attained maximum temperature during fall and early winter (~6-8 °C). Temperature gradients between the upper and lower water column in the spring and summer were associated with formation of the seasonal thermocline, which occurred in the upper 20 meters of the water column at most stations.

Freshening occurred in the near-surface (upper 20 m) during the portion of the year with the greatest incident sunlight, air temperatures, and snow melt runoff (May-September) (Figure 3). Salinity was highest during March and April. Minimum salinities occurred during July and August when a pronounced halocline formed within the upper 20 m of depth. In late fall and

winter months, salinities had a range of ~29-31 across the water column with a freshwater lens confined to the upper 10 m.

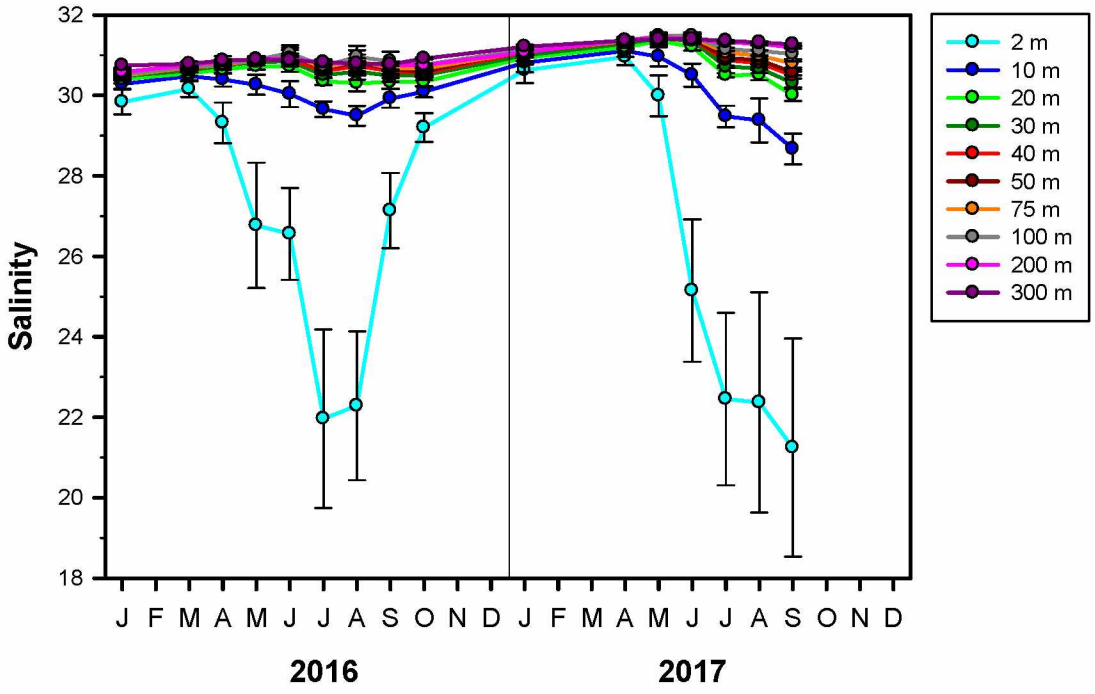

Figure 3. Mean salinities for selected depths at core oceanographic stations in Glacier Bay shown in Figure 1. Standard error bars indicated in black.

During April and May 2016, salinity was ~4 higher at 200 m than at the surface. During July, the salinity difference between surface and subsurface increased to 9 (~22-31). By September 2016, the bay's halocline weakened, and the surface began to salinize. The winter water column further de-stratified until May 2017, when stratification began to develop again. The minimum salinity in 2017 for the near-surface occurred during September at ~21, with a difference of 9.5 between the surface and depth (Figure 3). It is notable that the major thermoclines and pycnoclines were not co-located in both years. Generally, waters were colder, with greater stratification evident during 2017 than during 2016.

The differences in density between the surface and 20 m confirm stratification began from April to May of both years, and peaked during summer (Figure 4). Stratification persisted until weakening during September and October of 2016, but was still strong at most stations during September 2017. The outermost stations (Stations 1 and 24), closest to the sill, were typically the least stratified stations, a consequence of the extremely high currents and strong mixing that occurs over the sill.

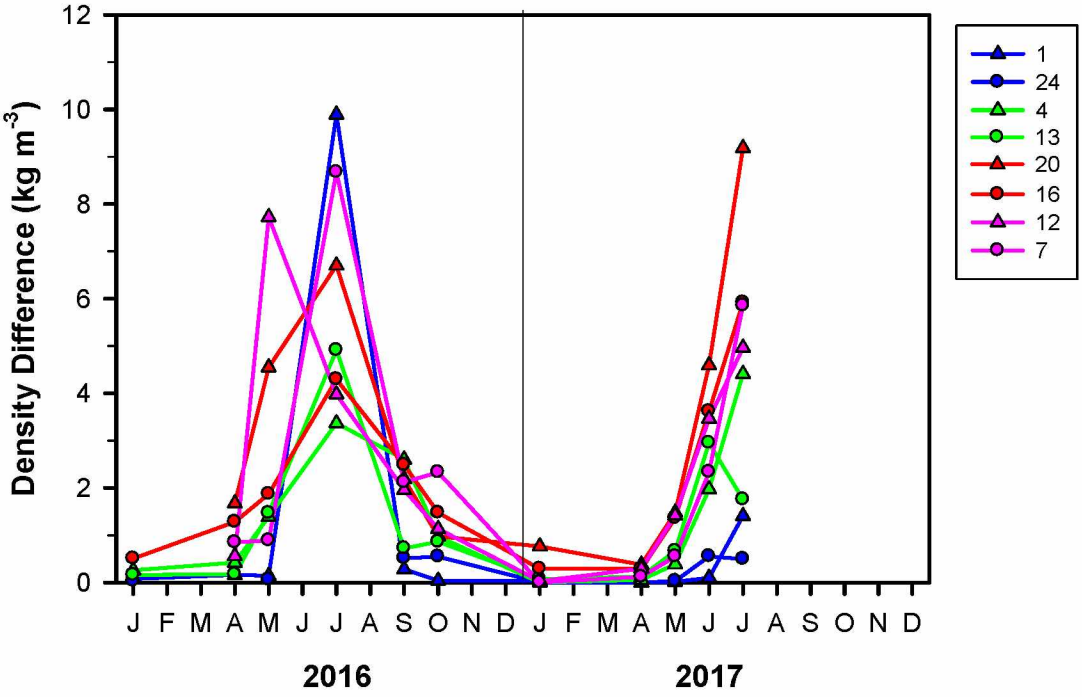

Figure 4. Stratification Index at core stations in Glacier Bay, utilizing the difference in density at 2-20 m. Symbols represent station numbers.

The seasonal cycle of nitrate in Glacier Bay shows maximum concentrations throughout the water column during winter (Figure 5), with similar values (18-24 µM) during January of 2016 and 2017. Glacier Bay's East Arm and West Arm generally show relatively consistent nutrient concentrations within all seasons (data not shown). During April to September of 2016

nitrate concentrations declined significantly at 2 and 10 m depth (2-18 µM) relative to January (~22 µM), with the lowest concentrations observed in July.

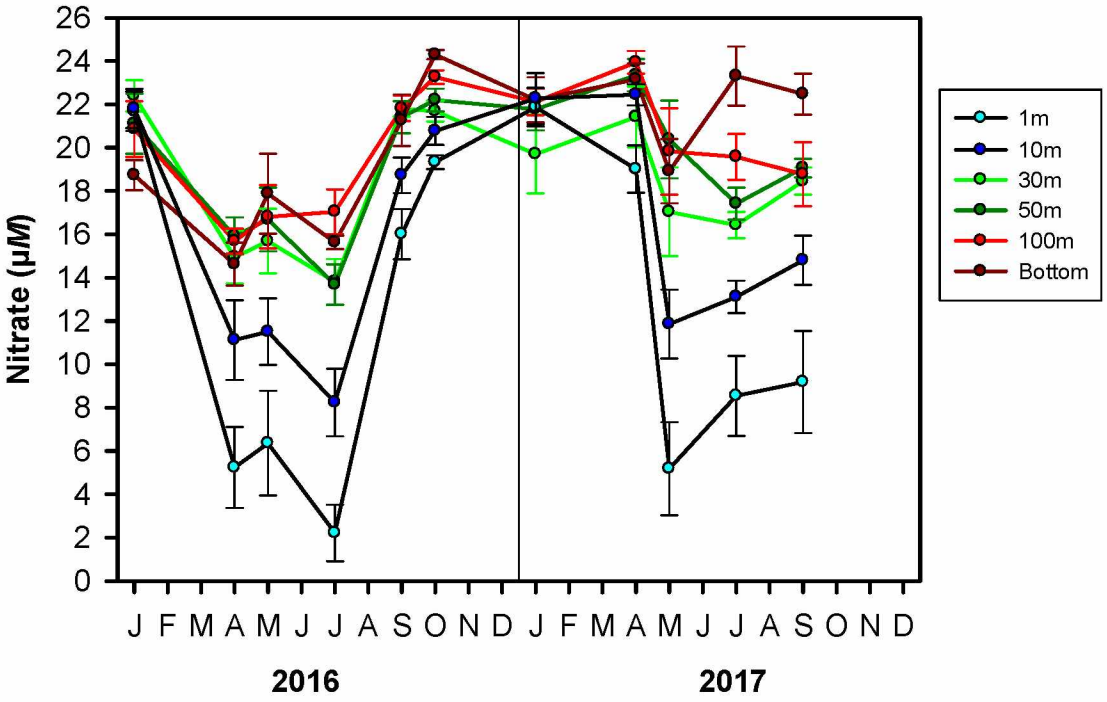

Figure 5. Nitrate concentrations averaged across core sampling stations in Glacier Bay shown in Figure 1.

Deeper waters (30-100 m) exhibited lower concentrations during April, May, and July 2016 (~15-17 µM) compared to winter months (~19-24 µM). Relative to 2016, the drawdown of surface nitrate in spring 2017 was delayed into May, which was the month with the lowest nitrate concentrations that year (~5 µM at 2m and ~12 µM at 10 m). Higher nitrate concentrations (~8-15 µM) were observed during July and September 2017 at these shallower depths, but compared to 2016, September 2017 had lower nitrate in the uppermost 10 m. The macro-nutrient data suggest that the Glacier Bay surface waters have the potential to become limited by nitrate rather than phosphate (e.g., West Arm N:P ratios ranged 10:1 to 14:1 compared to the Redfield ratio of 16:1) during periods of rapid growth. However, surface waters were never depleted of nitrate, even during the phytoplankton growing season. The lowest nitrate concentrations observed in

July 2016 (< 2 μM) at 2 m were associated with a pronounced freshwater lens at several locations, rather than with high biomass.

There was considerable spatial and temporal variability in integrated chlorophyll-*a* throughout the bay (Figure 6), but we found elevated levels (> 2 mgm^{-3}) at multiple stations during each sampling month between May and August.

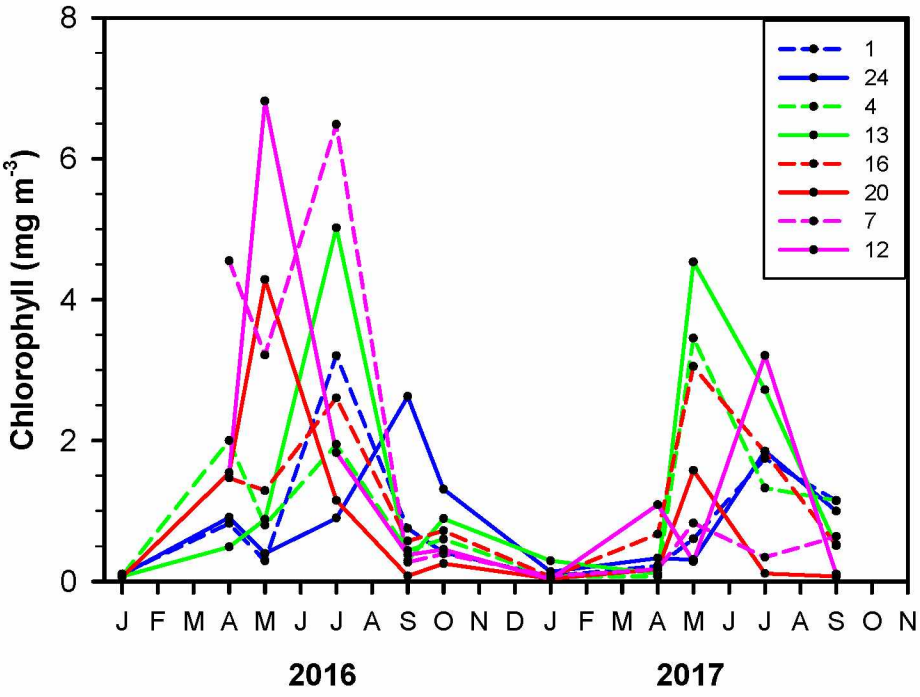

Figure 6. Average depth-integrated chlorophyll-*a* concentrations in Glacier Bay at core eight stations shown in Figure 1.

Late spring chlorophyll peaks were highest at the Glacier Bay terminal station (Station 12) during May 2016, whereas the May 2017 chlorophyll peak occurred within the central bay (Station 13). Chlorophyll was generally higher during the spring of 2016 than for 2017, while concentrations were higher during September of 2017 than 2016, this higher biomass is likely responsible for the lower nitrate concentrations in September 2017 compared to 2016. The earlier onset and duration of the phytoplankton growing season in 2016 was concurrent with warmer

sea-surface temperatures throughout the bay during 2016. Chlorophyll was appreciably lower at Stations 1 and 24 than in the rest of the bay during the spring and summer of 2016 and 2017.

Zooplankton

Total zooplankton abundance increased dramatically during late spring and summer then declined during the fall and winter (Figure 7). Throughout the bay, and in all seasons, copepods led in abundance, comprising 75 % of total zooplankton community. Copepodite abundance peaked during July 2016 and 2017 to ~15,300-16,700 indiv. m^{-3}, however, copepod naupliar abundances during spring were comparable to copepodites, especially for May 2017 when naupliar numbers exceeded copepodites (Figure 7). No other planktonic group rivalled copepod dominance within the bay, with the exception of September 2016 when abundances of copepodites and meroplankton both reached ~8000 indiv. m^{-3}. Non-calanoid zooplankters contributed 0-20 % of total zooplankton numbers for both years with the exception of the Lower Bay (Stations 01, 24) during the springs of 2016 and 2017 where meroplankton contributed ~25 % total zooplankton density, and during July 2016 when ~5-25 % of the zooplankton consisted of meroplankton. In terms of biomass, copepodites greatly exceeded all other zooplankton groups, however several other groups made notable contributions, such as chaetognaths during the spring and fall when they contributed ~13% during April 2016, ~8 % during September 2016, only ~8% during April 2017, and a dominating ~55 % of total zooplankton biomass during September 2017. Other zooplankton groups that had ephemeral signals or made minor contributions to biomass included: larvaceans, chaetognaths, euphausiids, ostracods, mysids, amphipods, and pteropods (Table 1, Appendix I).

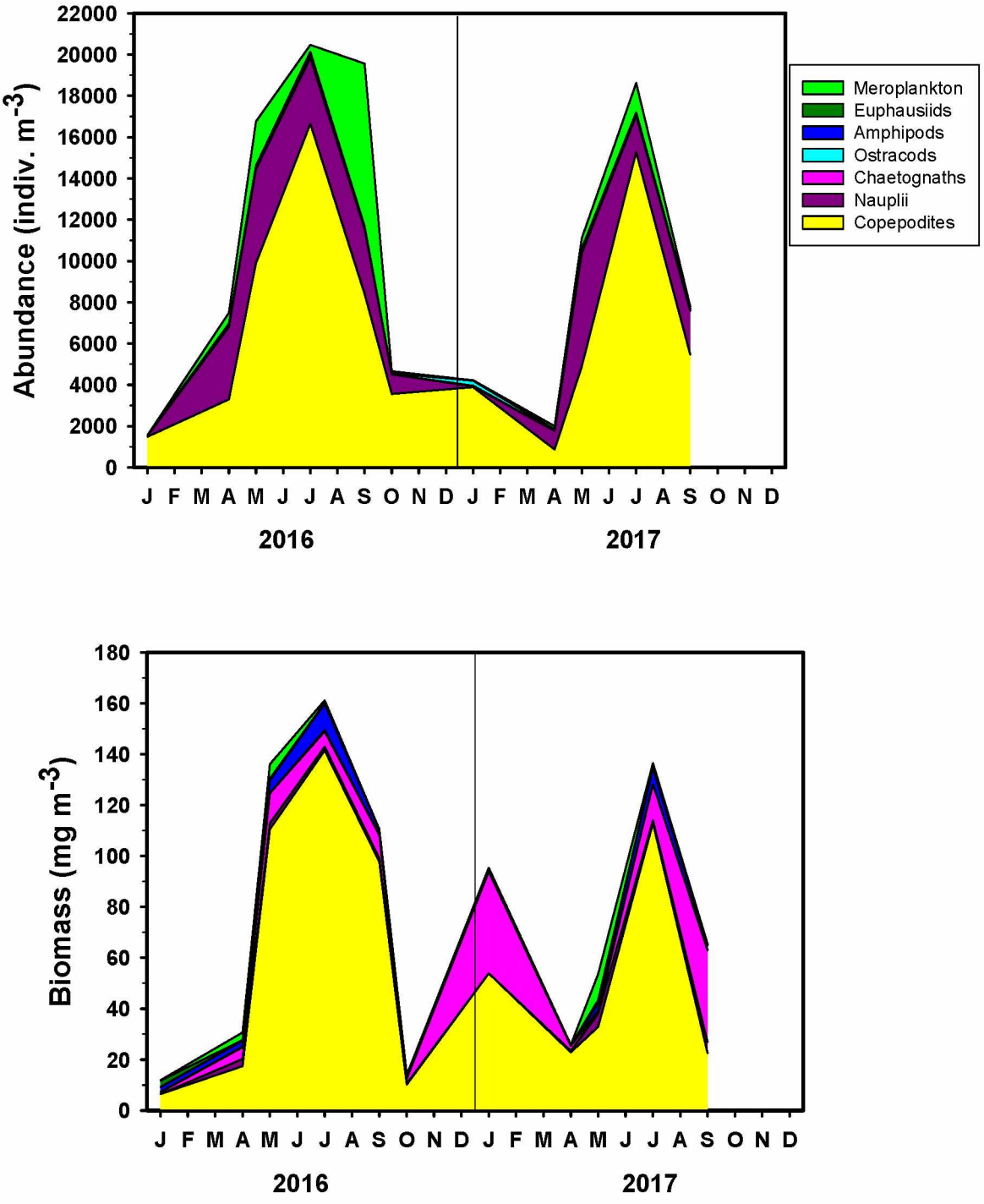

Figure 7. Seasonal patterns of major zooplankton group abundance and biomass averaged across core sampling stations within Glacier Bay. Top graph shows abundance of most prominent zooplankton, bottom graph shows

biomass of most prominent zooplankton. Zooplankton analysis from October 2017 was excluded because no physical data, chlorophyll, or nutrients were collected.

Table 1. Average abundance and biomass and frequency of occurrence of top twenty taxa identified based on frequency of appearance. UC upper water column (0-50 m), LC lower water column (50-180 m).

Top 20 taxa or species	Abundance (indiv. m^{-3}) UC	Abundance (indiv. m^{-3}) LC	Biomass (mg m^{-3}) UC	Biomass (mg m^{-3}) LC	Frequency of Occurrence UC	Frequency of Occurrence LC
Pseudocalanus (P. minutus, P. newmani, P. mimus)	3651	1271	11.31	6.55	84	63
Copepod nauplii	737	102	0.53	0.08	84	62
Metridia (M. okhotensis and M. pacifica)	337	632	17.54	44.52	78	63
Acartia longiremis	369	50	1.39	0.19	80	46
Oithona similis	891	280	1.1	0.34	84	63
Triconia borealis	222	123	0.29	0.19	71	62
Neocalanus (N. plumchrus, N. flemingeri, and N. cristatus)	18	5	1.39	0.15	25	14
Calanus (C. marshallae and C. pacificus)	4	5	0.48	0.91	52	46
Centropages abdominalis	7	6	0.08	0.18	23	31
Microcalanus pygmaeus	6	33	0.01	0.05	29	52
Harpacticoida	6	2	0.02	0	36	25
Ostracoda	21	81	0.03	0.14	44	47
Oikopleura labradoriensis	88	40	4.19	0.06	62	36
Limacina helicina	101	15	0.42	0.1	60	40
Parasaggitta elegans	22	4	6.34	2.9	77	61
Thysanoessa spp.	25	12	0.26	0.25	36	24
Bivalve larvae	591	46	0.19	0.02	61	32
Cirripedia	132	33	0.94	0.45	60	32
Cyphocaris challengeri	2	6	0.65	1.81	43	50
Polychaeta	41	20	0.21	0.12	36	26

The copepod community was dominated by multiple species of 6 genera: *Pseudocalanus* (primarily *P. minutus* and *P. newmani*), *Metridia* (*M. pacifica* and *M. okhotensis*), *Oithona* (*O. similis*), *Acartia* (*A. longiremis*), *Neocalanus* (*N. flemingeri* and *N. plumchrus*), and *Calanus* (*C. pacifica* and *C. marshallae*). Early copepodites could not be reliably separated to species in most cases, thus patterns were considered primarily at the generic level. All copepod genera displayed a seasonal cycle with highest abundances during late spring through early fall and lowest

abundances during winter (Figure 8). Most species abundances were greatest within the surface strata throughout the year, although numbers at depth became greater for *Pseudocalanus* and *Metridia* during the fall and winter, and for *Oithona* only during January.

Pseudocalanus dominated abundances in the upper water column with the largest peaks of *Pseudocalanus* occurring during July 2017 (~9000 indiv. m^{-3}). Naupliar stages had their highest numbers during May of both years and disappeared during winter. The naupliar peak during May 2016 (~5700 indiv. m^{-3}) was comparable to *Pseudocalanus* abundance during this month (~5800 indiv. m^{-3}). *Oithona* and *Metridia* abundances were similar in the upper stratum during July 2016 (2300-2400 indiv. m^{-3}). *Metridia* values in the upper stratum declined then remained low for the remainder of the year, peaking again during July 2017 at ~500 indiv. m^{-3}. *Oithona* numbers remained high during the fall, with ~1400 indiv. m^{-3} during September 2016, then became the most abundant copepod taxa during October 2016. *Acartia* reached its highest abundances during July 2016 (~1330 indiv. m^{-3}) and September 2016 (~840 indiv. m^{-3}) when salinity was lowest within the upper 20 m of the water column. *Pseudocalanus* and *Metridia* led in biomass contribution in the upper water column with ~15-60 mg m^{-3} in spring months of 2016 and 2017. Large-bodied *Neocalanus* contributed ~18 mg m^{-3} in upper column biomass during May of 2016, which is the third largest contributor to copepod biomass in this month.

Although *Pseudocalanus* dominated abundances within the 50-180 m lower stratum with peaks of ~2200 indiv. m^{-3} during July 2016, and ~ 2300 indiv. m^{-3} during September 2016, *Metridia* also contributed to a large portion of the community with ~1180 indiv. m^{-3} during July 2016 and ~790 indiv. m^{-3} during September 2016. In terms of biomass, however, the larger-bodied *Metridia* accounted for the larger portion of the lower stratum, with peaks occurring during July 2016 (~110 mg m^{-3}), January 2016 (~90 mg m^{-3}), and July 2017 (~50 mg m^{-3}),

compared to values below 20 mg m^{-3} for *Pseudocalanus* (Figure 9). Neither *Acartia*, *Neocalanus*, *Calanus*, nor *Oithona* made a noticeable contribution to abundance or biomass within the lower stratum (Figures 8 and 9).

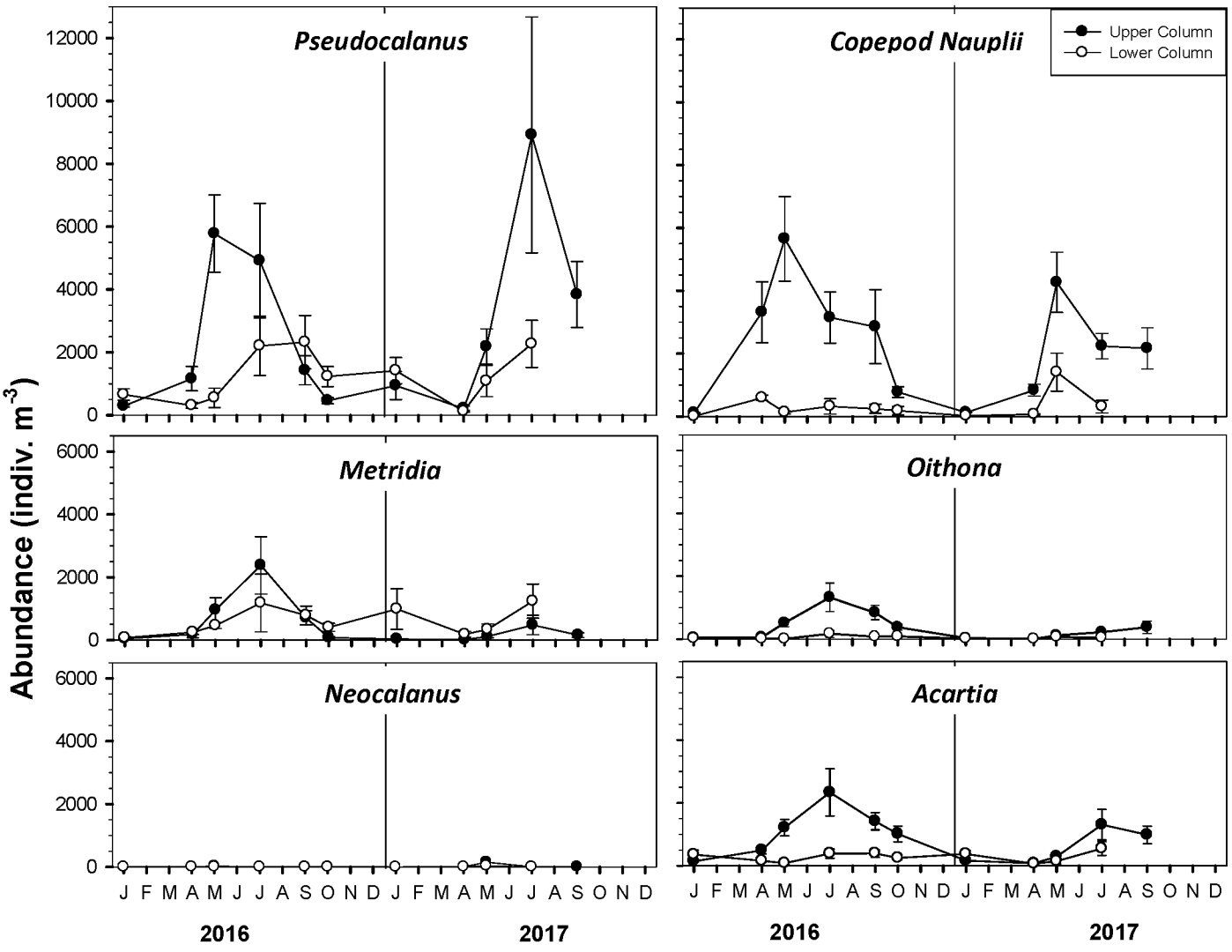

Figure 8. Seasonal patterns of major copepod abundance averaged across core sampling stations within Glacier Bay, delimited by upper (solid circle) and lower (open circle) depth strata.

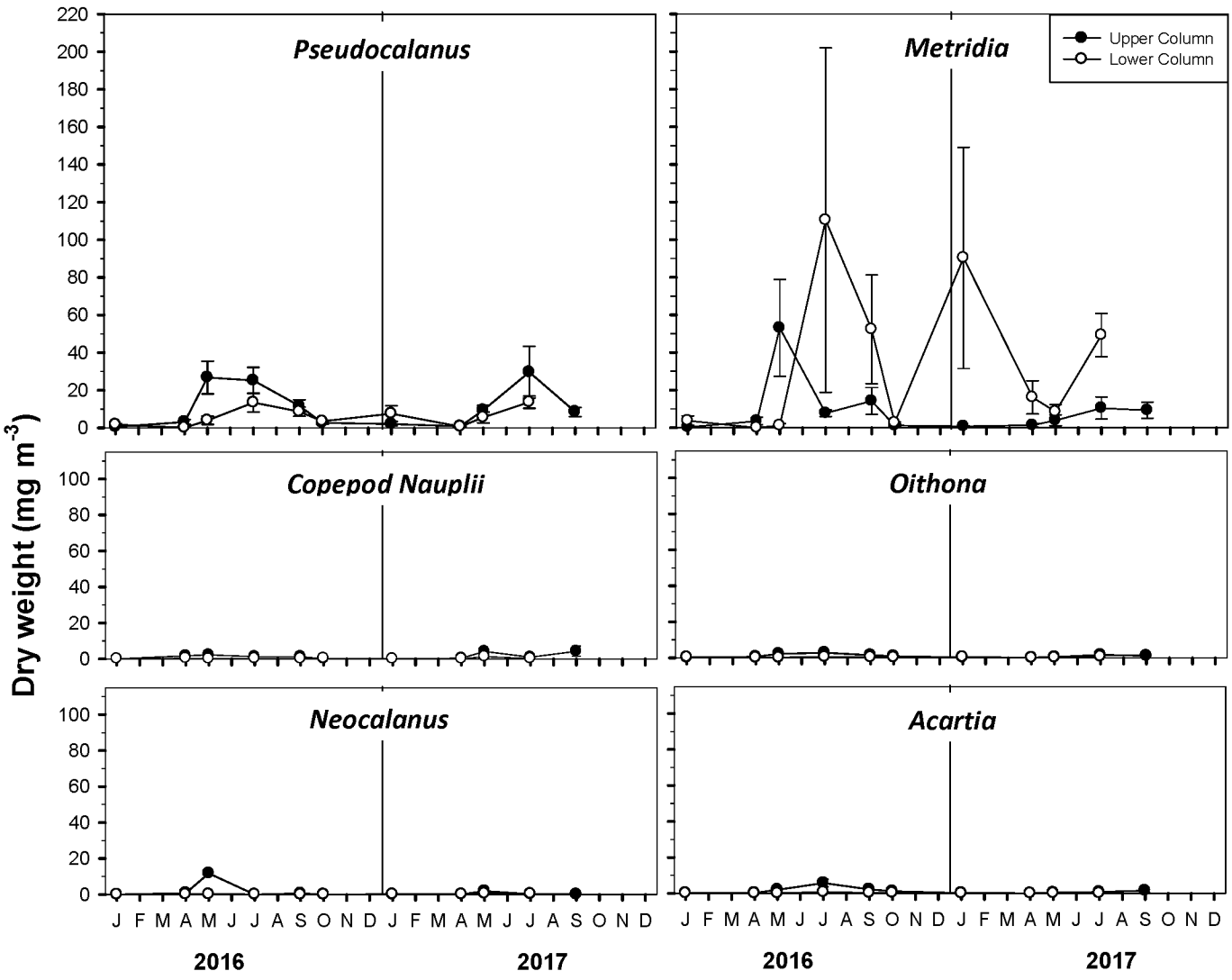

Figure 9. Seasonal patterns of major copepod biomass averaged across core sampling stations within Glacier Bay, delimited by upper (solid circle) and lower (open circle) depth strata

Zooplankton community patterns

Abundance

The most prominent pattern in zooplankton abundance was depth-related. Two distinct groups clustered out of zooplankton community abundance at 52% similarity, separating the majority of the upper stratum from lower stratum samples (Figure 10). Within those two depth-clusters, the second distinguishable pattern was season. At 57% similarity, three groups emerged:

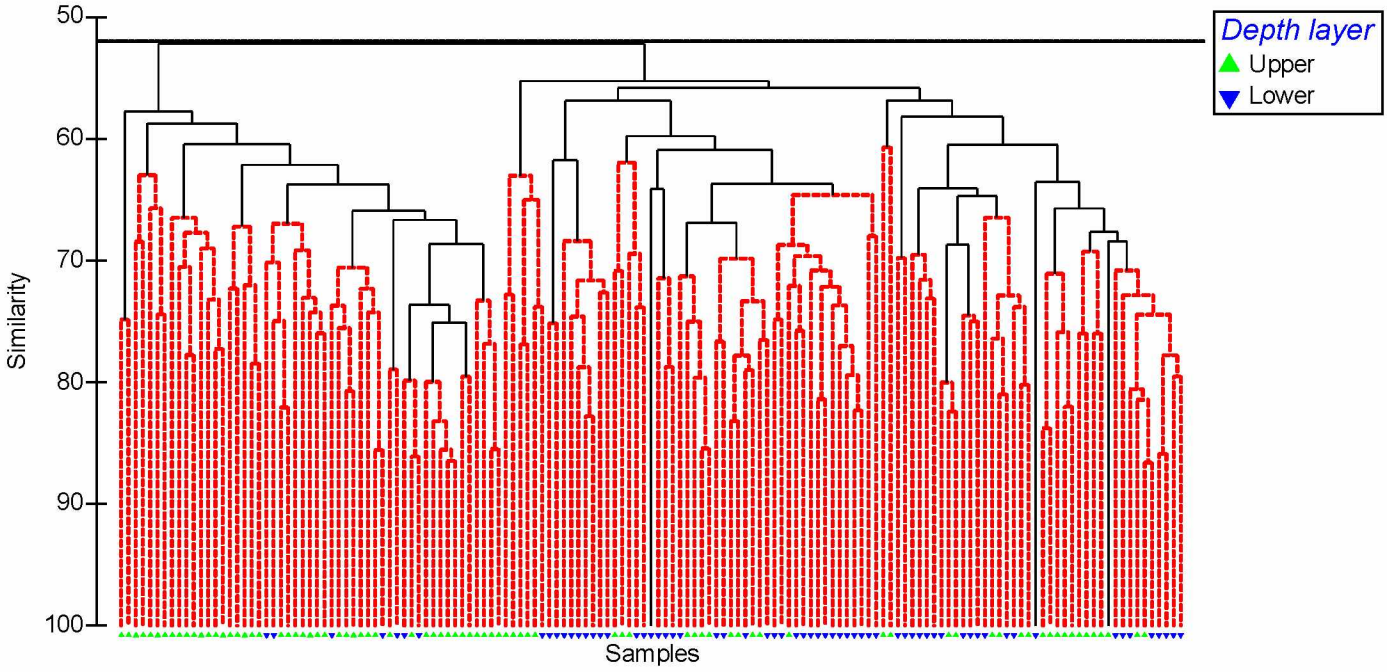

Figure 10. Clustering dendrogram of Bray-Curtis similarity using zooplankton abundances for upper and lower strata in Glacier Bay during 2016-2017. Slice indicated for 52 % similarity. Factor of separation shown as Depth.

winter months (January and April) separate from other months regardless of depth; upper stratum samples group together as months September, July, May, October, and some April; lower stratum samples group together as months July, September, October, and some May (Figure 10, 11). Subsequently, upper and lower strata samples were analyzed separately.

The upper stratum formed two main groups based on seasonal similarity; January and April 2017 separate from other sampling months, likely caused by colder, weakly stratified winter water influencing community structure (Figure 12). In analyzing the nMDS for upper stratum, spatial differentiation appeared in 2D nMDS between winter water (January, April 2017) and the other months, and calendar months of different years were often near each other (Figure 13). Although 2D stress was modest (0.22), 3D stress (not shown) was much lower (0.14). A seasonally cyclic pattern to the centroid of monthly values was also discernable (Figure 13). Lower stratum abundances did not show as distinct a seasonal pattern as the upper stratum (Figure 14). Four independent clusters occur; at 58 % similarity a winter water group (January, April, May samples) at termini stations 20 and 12 separate from two seasonal groups occurring at similarity 61 % where samples from mostly July, September, October samples part from April, January samples, however there are several intermingled outliers. Stress in 2D lower stratum abundance was high-modest (0.24), while 3D stress (not shown) was reduced (0.16).

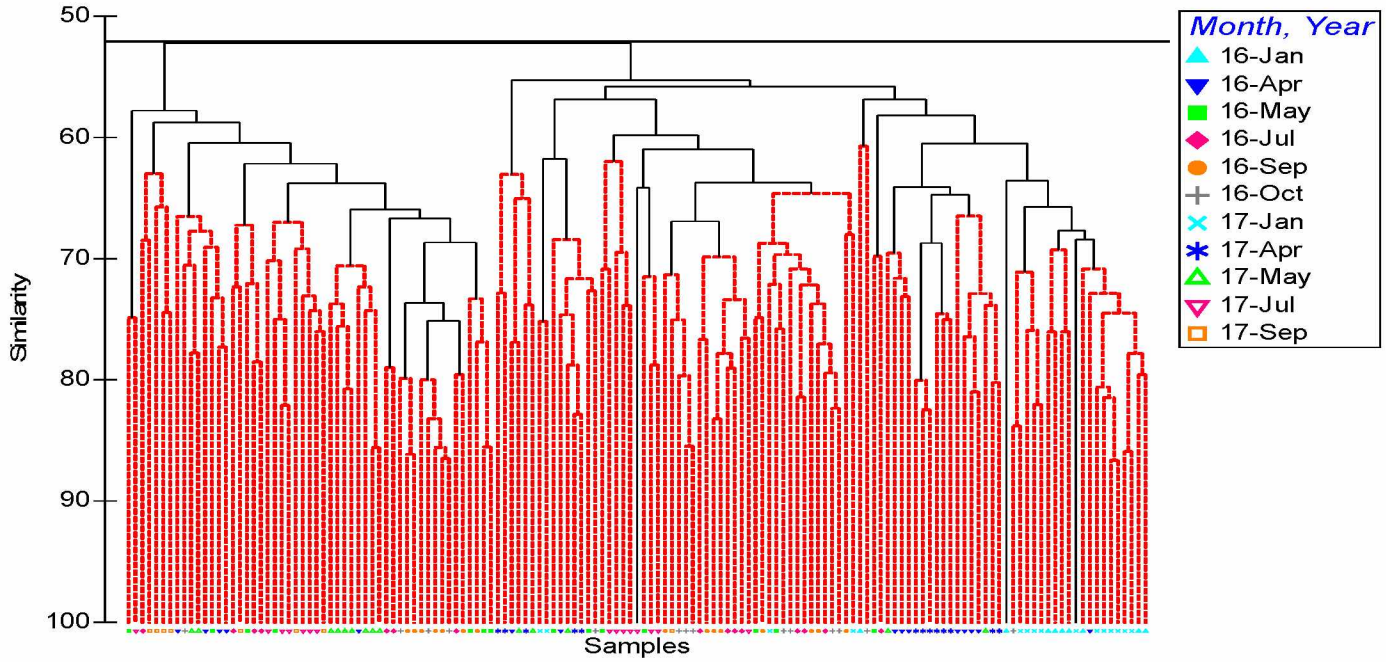

Figure 11. Clustering dendrogram of Bray-Curtis similarity using abundances for cruises (both upper and lower strata) in Glacier Bay during 2016-2017. Slice indicated for 52 % similarity. Factor separation shown as Year-Month.

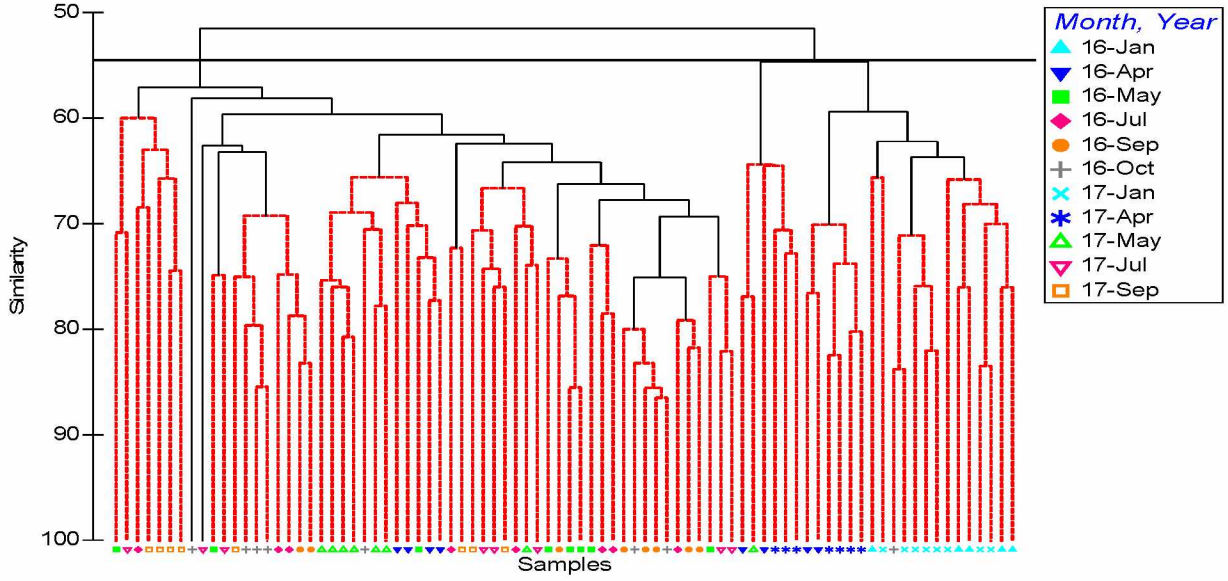

Figure 12. Clustering dendrogram of Bray-Curtis similarity using zooplankton abundances for upper strata in Glacier Bay during 2016-2017. Slice at 54.5 % similarity. Organized by Year-Month.

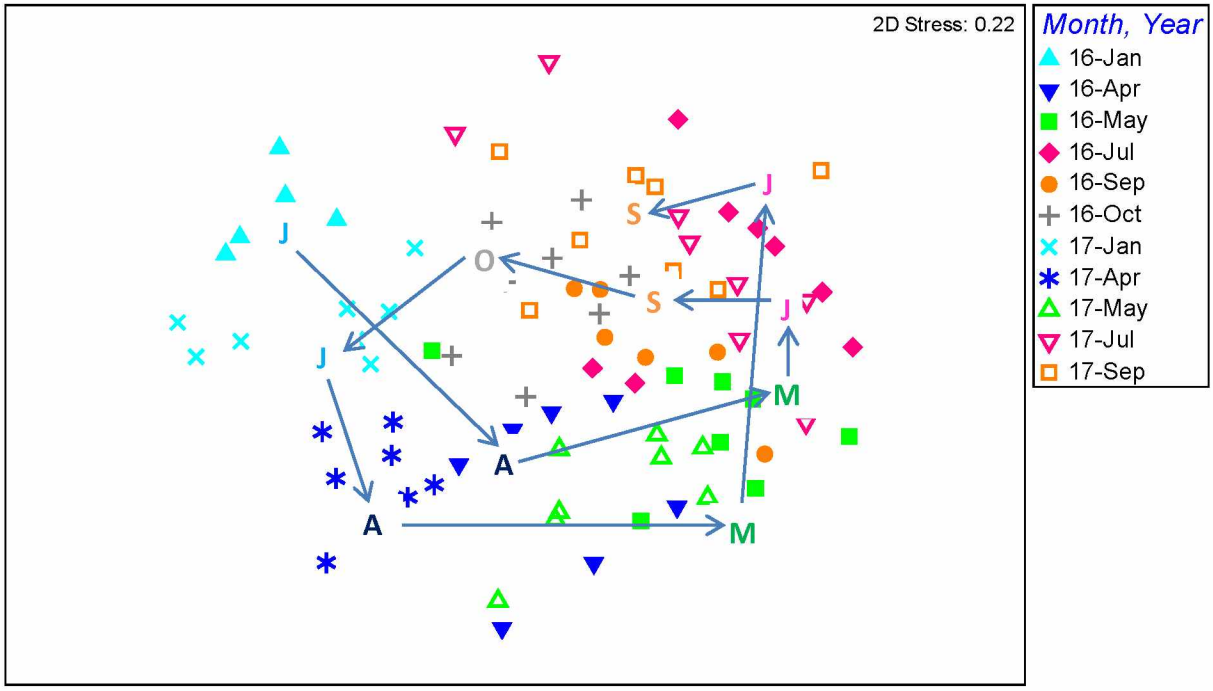

Figure 13. Non-parametric Multi-Dimensional representation of upper stratum zooplankton abundance separated by Year-Month. Beginning letter of each month represented depicted in the sample points from that month, arrows show the order by which samples were collected seasonally.

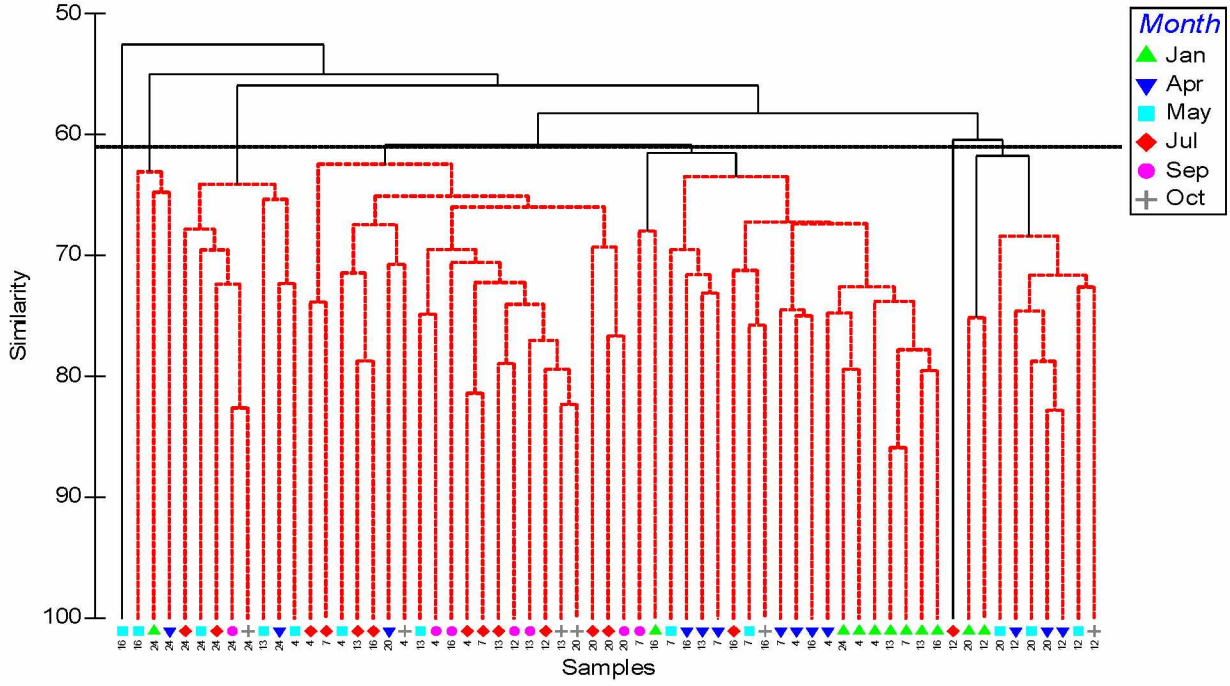

Figure 14. Clustering dendrogram of Bray-Curtis similarity using zooplankton abundances for lower strata in Glacier Bay during months of 2016-2017. Slice at 61 % similarity.

Biomass

Analysis on biomass similarity suggests a seasonal grouping before depth (Figure 15).

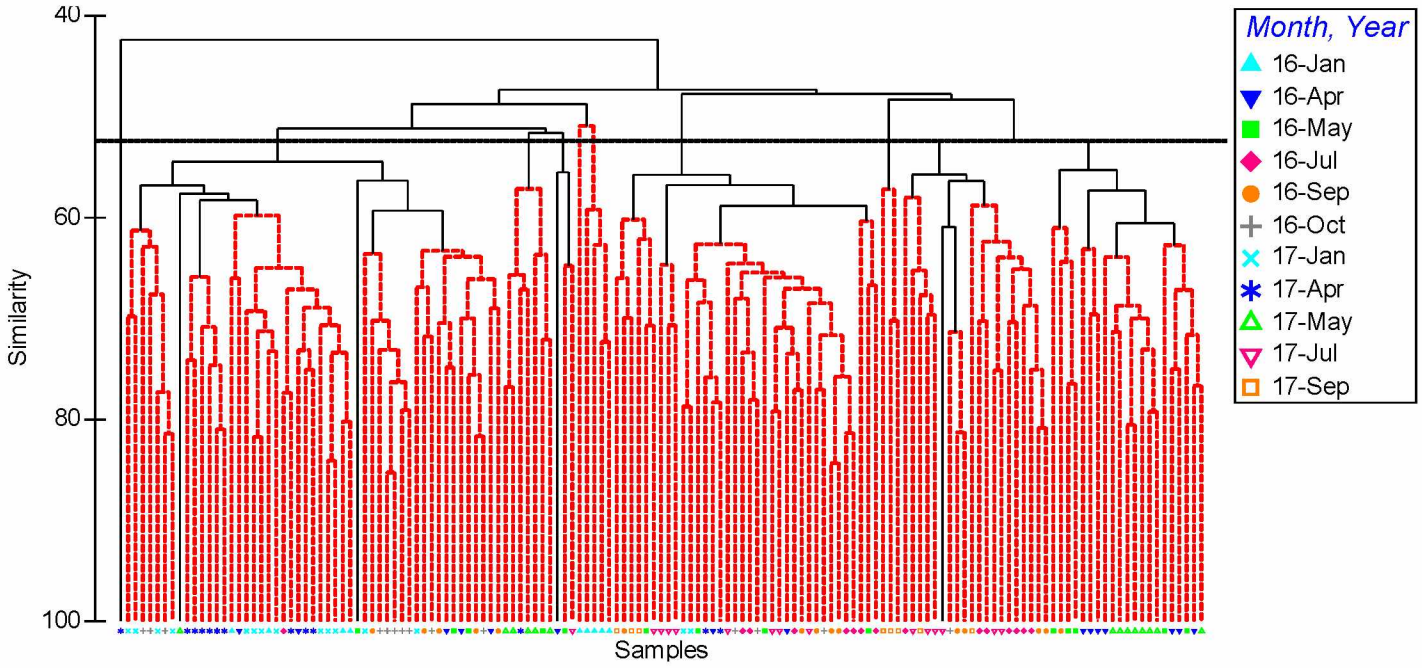

Figure 15. Clustering dendrogram of Bray-Curtis similarity using abundances for upper and lower strata in Glacier Bay during 2016-2017. Sliced at 52.5 % similarity to indicate cluster separation of summer/fall from spring months.

At 47.5 % similarity, one section separates including January, April, October, and some May samples. The other section contains a divide between a group of July, September, and some May/April, and a cluster group separating at 52.5 % similarity into a July/September group and an April/May group. At 47 % similarity a mix of depths in upper and lower strata are visible (Figure 16).

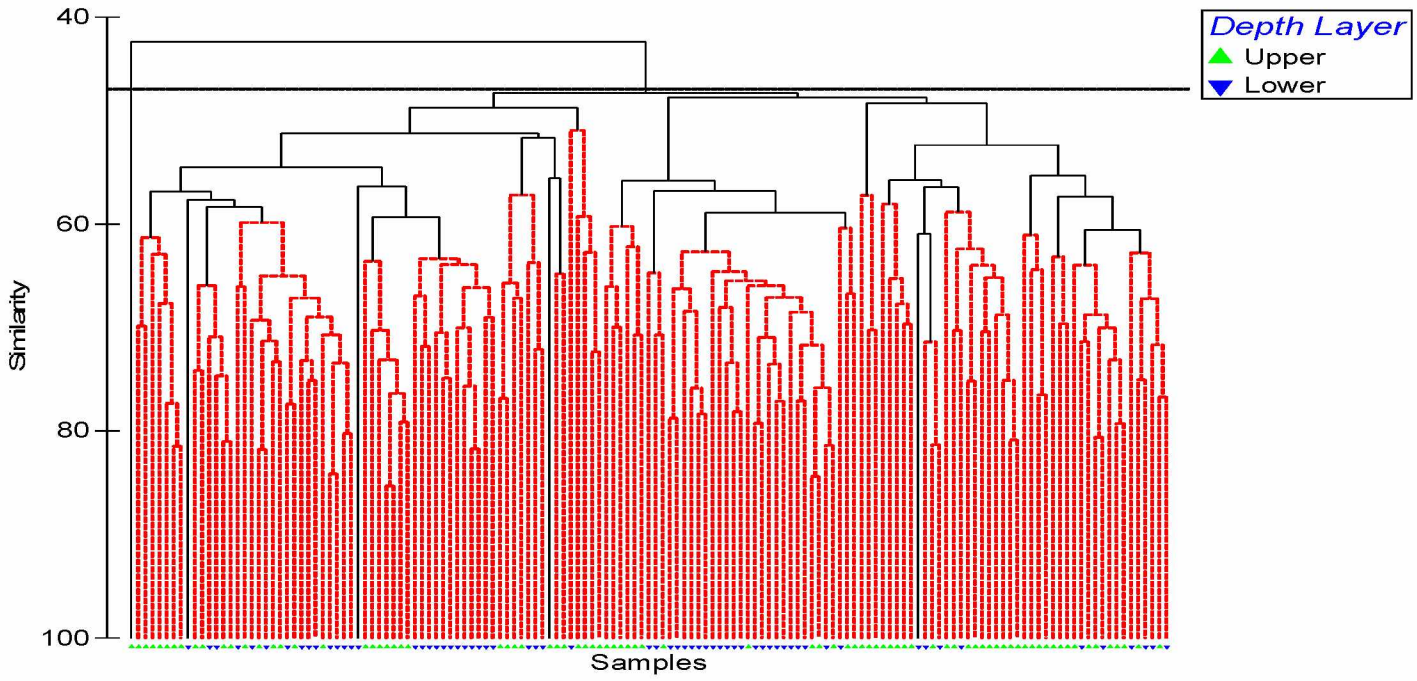

Figure 16. Clustering dendrogram of Bray-Curtis similarity using biomass for strata in Glacier Bay during 2016-2017. Sliced at 47 % similarity.

An nMDS analysis shows upper strata separates from the lower strata samples with a 2D stress of 0.24 and a 3D stress (not shown) of 0.17 (Figure 17). Reanalysis by water layers shows the upper stratum with significant seasonal structure. One cluster separates out first at 45.5 % similarity, containing January and a few October samples. Two other clusters part at 49 % similarity, dividing the upper strata of April and May from July, September, and October samples (Figure 18). A plot for nMDS in 2D shows some separation for the months of January and April 2016 in the upper stratum, January and April of 2017 does not overlap although they are in closer proximity than the previous year. Upper stratum stress for biomass in 3D nMDS is modest at 0.16 (not shown). Lower stratum biomass was analyzed separately for completeness, however, samples did not show much interpretable separation.

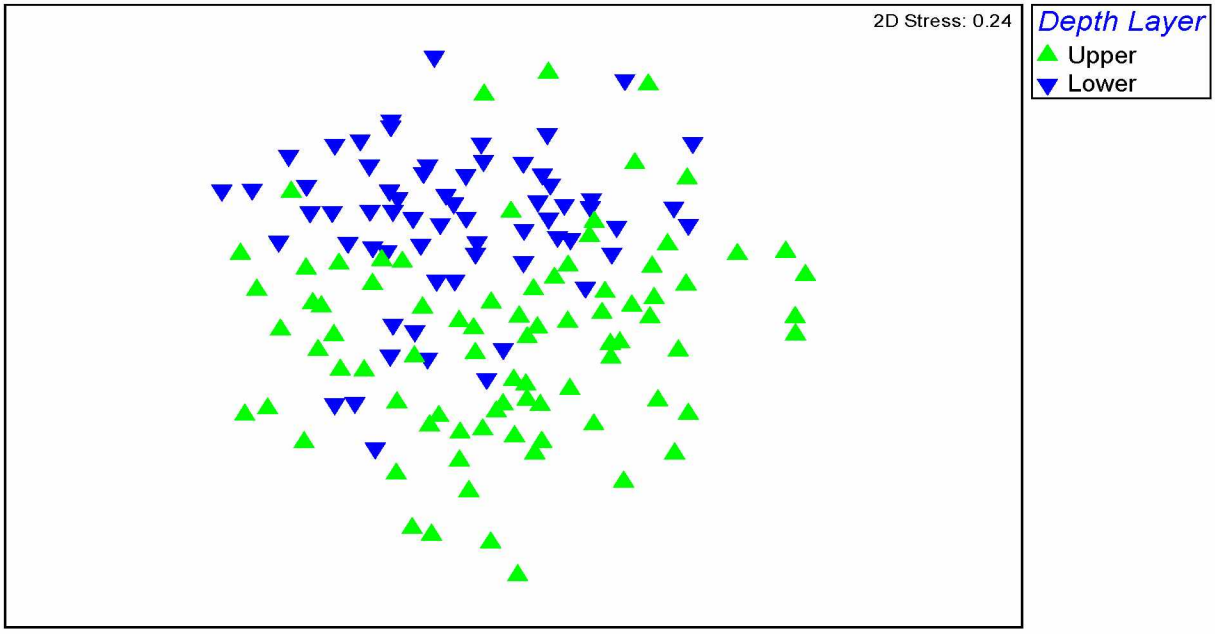

Figure 17. Non-parametric Multi-Dimensional Scaling representation of zooplankton biomass similarity from the upper and lower strata.

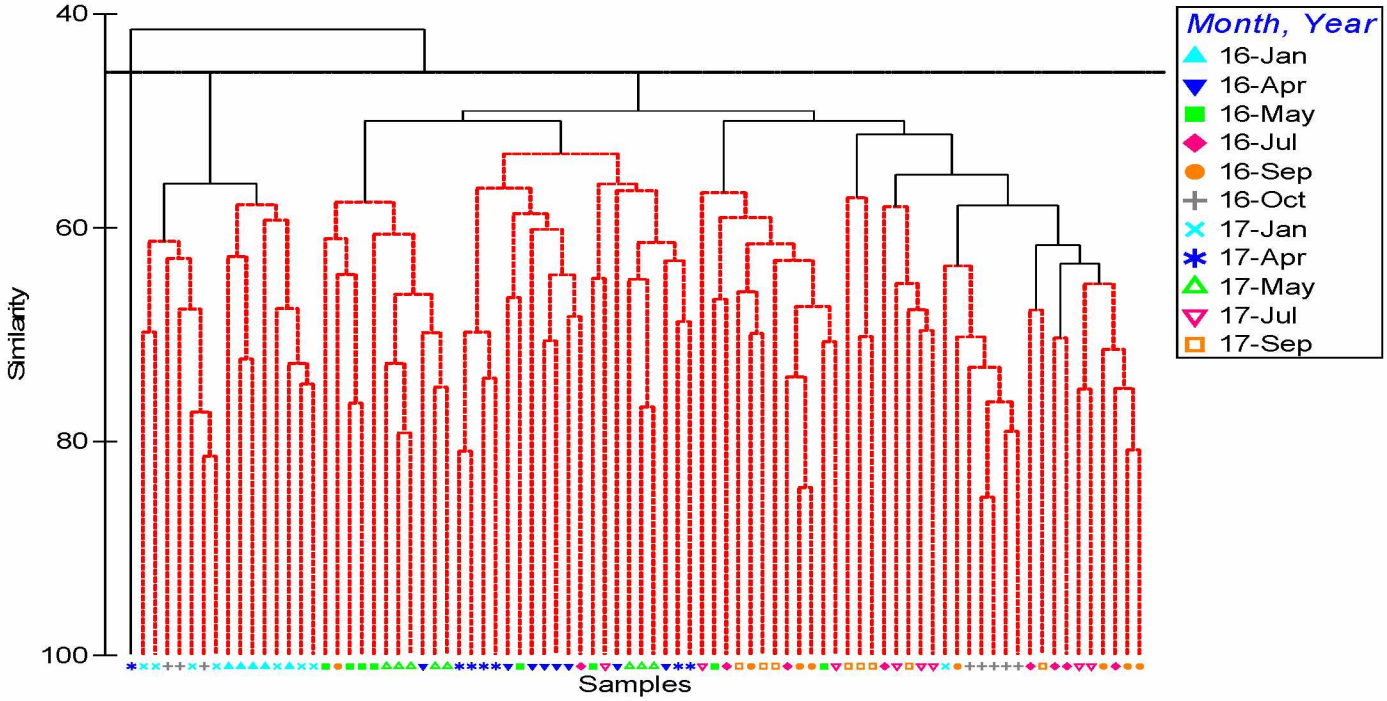

Figure 18. Clustering dendrogram of Bray-Curtis similarity using biomass for upper strata in Glacier Bay during 2016-2017. Sliced at 45.5 % similarity.

BEST Analysis

Correlations between zooplankton community structure and environmental variables were low to moderate. The variable combination explaining the most about zooplankton community structure in Glacier Bay's upper stratum was the single variable, temperature (T) and the combination of temperature and salinity (T, S) as the primary determining variables for abundance and biomass. T abundance correlation was 0.323 and T, S abundance correlation was 0.317, single variable T and combination T, S had the same correlation with regards to biomass 0.226 (Table 2). Correlations using BEST in the lower stratum identify salinity and temperature as the most correlated variables for both abundance and biomass. The highest correlation for biomass, however, was the single variable of salinity. T, S abundance correlation was 0.216, S biomass correlation was 0.223, and T, S as the second highest in correlation value for biomass was 0.196 (Table 3). Chlorophyll-a was somewhat surprisingly uncorrelated to zooplankton. There was no relationship to dissolved oxygen.

Table 2. Relationship between environmental variables and zooplankton in the upper (0-50 m) stratum samples; T (temperature), S (salinity), O (oxygen), C (chlorophyll). All correlations reported only for $p < 0.05$.

No. variables	Variable combinations with BEST analysis (Spearman rank correlation)			
Abundance				
1	T	S		
	0.323	0.185		
2	T, S	T, C	T, O	S, C
	0.317	0.233	0.232	0.148
3	T, S, O	T, S, C	T, C, O	
	0.268	0.258	0.178	
4	T, S, C, O			
	0.229			
Biomass				
1	T	S		
	0.226	0.179		
2	T, S	S, C	T, O and T, C	S, O
	0.226	0.16	0.149	0.131
3	T, S, O	T, S, C		
	0.221	0.215		
4	T, S, C, O			
	0.176			

Table 3. Relationship between environmental variables and zooplankton in the lower (50-10 m above seafloor) stratum samples; T (temperature), S (salinity), O (oxygen), D (depth).

No. variables	Variable combinations with BEST analysis (Spearman rank correlation)			
Abundance				
1	S	T		
	0.203	0.139		
2	T, S	S, O	T, O	S, D
	0.217	0.198	0.147	0.102
3	T, S, O	T, S, D	S, O, D	
	0.198	0.135	0.092	
4	T, S, O, D			
	0.131			
Biomass				
1	S	T		
	0.223	0.101		
2	T, S	S, O	S, D	T, O
	0.196	0.177	0.136	0.13
3	T, S, O	T, S, D	S, O, D	
	0.186	0.139	0.119	
4	T, S, O, D			
	0.142			

Discussion

This study provides the first multi-seasonal description of the zooplankton community structure for Glacier Bay, Alaska, contributing to the paucity of what is known about high-latitude Pacific fjord ecosystems. Our results show general coherence with adjacent shelf communities of the Gulf of Alaska (GoA) and Icy Strait that follows typical higher-latitude seasonal patterns where cold, nutrient-rich winter waters support a spring phytoplankton bloom driven by increasing light and subsequent stratification, followed by increases in zooplankton that persist into fall (Coyle and Pinchuk, 2005; Park *et al.,* 2004; Strom *et al.*, 2006). These patterns are also typical of other high latitude fjords in the northern hemisphere across Greenland (Arendt *et al.*, 2013, 2016; Swalethorp *et al.*, 2014), Iceland (Weslawski *et al.*, 1991), and British Columbia (Mackas *et al.*, 2001; Tommasi *et al.*, 2012).

As an isolated estuarine fjord, Glacier Bay is surrounded by a steep mountainous landscape, complete with ice fields and twelve tidewater glaciers (Etherington *et al.*, 2007). Freshwater sources to the bay are from glacial and snow melt including numerous streams that account for salinity and temperature distributions (Danielson, 2012; Hill *et al.*, 2009). Using BEST analysis to account for salinity and temperature as numerical environmental factors in Glacier Bay, we found temperature (T) as the significant factor in the upper stratum and salinity (S) as the significant determining factor in the lower stratum. The bay's surface goes through annual cycles of freshening, stratifying the upper layers with cold, fresh runoff in summer and fall, and subsequently mixing with deeper waters. With little change in T in subsurface waters, annual deep water replenishment appears to make salinity a lower stratum community determinant. Strong tidal currents over several relatively shallow sills help promote nutrient exchange across the pycnoclines via enhanced mixing (Etherington *et al.*, 2007). These nutrient

inputs appear to be sufficient to sustain high phytoplankton biomass throughout spring and summer and into early fall.

Temperatures on average are colder, and surface waters fresher, within Glacier Bay (Etherington et al. 2007) than the GoA (Coyle and Pinchuk, 2003, 2005) or Icy Strait (Park *et al.*, 2004). Although nitrate shows surface drawdown during the spring bloom (Reisdorph and Mathis, 2015), it is seldom reduced to concentrations known to limit phytoplankton growth (~2 μM- Strom *et al.*, 2006). Patterns in nutrient availability throughout surface waters thus explain the high chlorophyll concentrations (i.e., 1-7 mg m^{-3}) observed at nearly all stations throughout the summer and into fall. These high chlorophyll concentrations in turn support zooplankton abundances of ~20,000 indiv. m^{-3} and biomass of ~135-160 mg DW m^{-3}, both of which are higher than reported outside the bay (Coyle and Pinchuk, 2003, 2005; Park *et al.*, 2004; Sousa *et al.* 2016). Our observations show that during peak months of zooplankton production within Icy Strait and Glacier Bay (May-July), Icy Strait communities contained mean abundances of only ~775-1,850 indiv. m^{-3} of copepods, whereas Glacier Bay recorded abundances were ~4000-16,000 indiv. m^{-3} (Park *et al.*, 2004; Figure 7, 8).

Outside the bay, on the GoA shelf and in the PWS fjordal system, chlorophyll concentrations typically reach a maximum during April or May, reducing to lower concentrations by July (Strom *et al.*, 2006; Figure 6), and drive the seasonally varying zooplankton community compositions. *Neocalanus* copepods dominate across the shelf in the GoA and in PWS, during April and May. *Metridia* and *Calanus* also begin to increase in numbers during May, but transition to a numerical dominance of *Pseudocalanus* during July and August (Coyle and Pinchuk, 2005). Icy Strait communities showed peak zooplankton production in May-July, analogous to adjacent communities in Glacier Bay (Park *et al.*, 2004).

Seasonal and spatial variations in Glacier Bay were substantial both in terms of abundance and biomass of zooplankton. Congruent with studies done in the GoA, and adjacent Icy Strait, *Pseudocalanus* is a significant player within the zooplankton community of Glacier Bay, and an important prey item for juvenile and larval fishes (Kendall and Nakatani, 1991; Napp *et al.*, 1996; Cooney *et al.,* 2001; Napp *et al.*, 2005; Coyle and Pinchuk 2003, 2005; McKinstry and Campbell, 2018). *Pseudocalanus* life history is strongly influenced by temperature, preferring the colder water (< 15 °C) of temperate through subarctic neritic shelves (Lee *et al.*, 2003; Morgan *et al.*, 2003; Napp *et al.*, 2005). Glacier Bay provides prime habitat for the suspension feeding *Pseudocalanus*, especially within the spring-late summer surface waters. Between May and September of 2016 and 2017, *Pseudocalanus* abundances were highest in the upper stratum throughout the bay (~2500-9000 indiv. m^{-3}). Copepod nauplii additionally made significant numerical contributions to the bay's upper stratum during the spring phytoplankton bloom, with reduced presence by summer and fall. The size distribution and morphology of nauplii suggests most belong to *Pseudocalanus.* This is consistent with the peaks in *Pseudocalanus* reproduction typically associated with the spring bloom during May, with reduced but sustained egg production throughout the summer (Napp *et al.*, 1996).

Despite the prominence of *Pseudocalanus* in copepod abundances within Glacier Bay, *Metridia* was the taxa dominating copepodite biomass. Also commonly found in GoA's deeper neritic environments, later-staged *Metridia* undergo diel vertical migration on a nightly feeding schedule (Batchelder, 1986; Osgood and Frost, 1994; Dagg *et al.,* 1997; Coyle and Pinchuk, 2005; Sousa *et al.*, 2016). On the NE Pacific coast of Washington, *Metridia* stays below 75 m depth during daylight hours (Osgood and Frost, 1994; Dagg *et al.*, 1997). *Metridia* filter-feeds on protists and microzooplankton such as calanoid nauplii and early-stage small copepods

(Vestheim *et al.*, 2013), making spring and summer prime time for its abundance in the bay. As larger-bodied copepods, *Metridia* contribute the greatest dry weights for zooplankton within the bay, especially within the lower stratum (up to 115 mg m^{-3}), despite numbers lower than *Pseudocalanus* by a factor of 3 (Figures 8 and 9). Other copepods of note included: *Acartia*, a neritic species that is common in estuaries (Cervetto *et al.*, 1999; Park *et al.*, 2004; Magalhaes *et al.*, 2009; McKinstry and Campbell, 2018); the ubiquitous cyclopoids, *Oithona* and *Triconia* that are found in the bay year-round with low abundances; and various meroplankton that occur primarily during the summer and fall. Both cyclopoids and meroplankton can be major players in other isolated systems and on shelves in the arctic and sub-arctic where salinities are lower and temperatures rise during summer (Cairns, 1967; Weslawski *et al.*, 1991; Incze *et al.*, 1996; Cooney *et al.*, 2001; Tommasi *et al.*, 2012; Swalethorp *et al.*, 2014; Arendt, 2016; Gluchowska *et al.*, 2016; Sousa *et al.,* 2016).

A notable departure from the zooplankton communities of the open GoA is the brief and muted signal of large-bodied copepods such as *Calanus* and *Neocalanus*. The degree of "openness" of the fjord greatly influences abundances of zooplankters within the system (Willis *et al.*, 2006; Skreslet *et al.*, 2015). Open fjords, unimpeded by sills or land mass, are thought to host zooplankton species largely advected into the system, while more closed or sheltered fjords may have greater influence from local production (Bucklin *et al.*, 2000). Thus, Hornsund fjord, Isfjorden, and Kongsfjorden on the western shelf of Svalbard which are largely open to Atlantic and Arctic currents, contain token shelf pelagic species of *Calanus*, Euphausiids, and others (Basedow *et al.*, 2004; Gluchowska *et al.*, 2016). In contrast, fjords like those of Godthabsfjord, Greenland (Swalethorp *et al.*, 2014), and Rivers Inlet, British Columbia (Tommasi *et al.*, 2012), have land masses or shelves obstructing their entrances, impeding exchange and thereby favoring

localized estuarine and neritic specific copepods. The shallow sill at the entrance of Glacier Bay and its estuarine circulation appear to generally discourage the inward advection of *Neocalanus* that dominate the GoA ensemble during the spring and early summer (Incze *et al.*, 1996; Coyle and Pinchuk, 2005; and Cooney *et al.*, 2001). Additionally, life histories of *Neocalanus* species involve summer decent well below 500 m to enter diapause (Miller *et al.,* 1984; Miller and Clemons, 1988). Although our nets did not fish deeper than 180 m to track such migrations, we did not observe significant abundances of *Neocalanus* in the lower and central bay beyond April, and the limited habitat in the bay between 400 m and its maximum of ~450 m suggests that *Neocalanus* do not have a resident population. Even *Calanus,* which is successful in other nearby fjordal habitats such as PWS (McKinstry and Campbell, 2018) and British Columbia (Tommasi *et al.*, 2012), remains scarce within Glacier Bay.

Using the multivariate approach, we characterize the zooplankton community as a whole; the upper and lower strata cluster showed two major separation factors: depth, and time. There was a significant separation of the upper and lower strata driven by difference in zooplankton community composition between these depths (Figure 10). It is notable that the degree of separation between the upper and lower strata communities is evident in the daylight hours within the bay, but might be weaker at night when diel migration of zooplankton such as *Metridia* occurs (Dagg *et al.*, 1997). The second major multivariate factor was temporal, specifically described as Year-Month. Three sample groups are evident within the separately analyzed upper and lower strata: a winter group consisting of January and April 2016 and 2017 samples; a summer-fall group that includes samples from July and September of both 2016 and 2017, plus October 2016; and a terminal bay group that included glacial termini locations (Stations 12 and 20) with a few fall and spring occupations within the east arm (Station 16). This

unique terminal station set includes both upper and lower strata samples intermingled as a group of outliers that suggest a unique glacial-specific well-mixed community that inhabits the bay year-round.

Non-copepod zooplankton within the bay contribute a minor portion of zooplankton abundance and biomass annually (lower bay Stations 1 and 24 are exceptions for meroplankton). Although minimal in a numerical sense, they include meso- and macrozooplankton (sized 0.2-20 mm and 20-200 mm) that act as important predators and omnivores within the plankton community, and as prey items for higher level predators. Larvaceans, for example, have been found to be bacterivorous utilizing their filter-feeding technique, connecting to the lowest planktonic link (King *et al.*, 1980). Euphausiids are omnivorous, feeding on detritus, diatoms, echinoderms, amphipods, cheatognaths, and copepods depending on the species (Sogawa *et al.*, 2016). Ostracods are omnivorous, filter-feeding detritivores, bacterivores, and grazers (Fernandez *et al.,* 2016); whereas the filter-feeding diet of *Limacina helicina* (pteropod) consists largely of smaller copepods, tintinnids, and diatoms (Gilmer and Harbison, 1991). The notorious zooplankton predator, the chaetognath, is abundant in many marine systems and is often caught with larger mesh sized nets (i.e., 333 µm mesh) (Baier and Purcell, 1997). The fact that we used a 150 µm mesh net, collectively focused on the bulk of the community in the mesozooplankton (0.2-20 mm) size range. No doubt some of the larger species (e.g., euphausiids, amphipods, chaetognaths) in the bay are under-sampled by our use of relatively small-mouthed nets, and exclusively daytime sampling—logistics determined by the capabilities of our sampling platform.

Although this study is novel for Glacier Bay in terms of zooplankton sampling, this fjord has over two decades of physical data monitored at these oceanographic stations. Our

observations throughout the bay indicate a warm water anomaly occurring during 2016 compared to average temperature cycles in the bay (Danielson, 2012; Etherington *et al.*, 2007). Looking at late winter and spring months of 2016 (Mar-May), the entire water column was 0.5-2 °C above, increasing to 1.75-2.5 °C above normal in the upper 100 m, and still above average in the lower stratum during late summer (August-September). Generally, salinity values were within the typical range (~27-31) observed within Glacier Bay during spring, but at times lower by ~5 units in the upper 20 m due to freshwater inputs. A study done in adjacent Icy Strait, discusses El Niño and La Niña Southern Oscillation events over 1997-98, showing anomalously warm temperatures associated with El Niño throughout the region including Glacier Bay (Whitney *et al.*, 1999; Park *et al.*, 2004; Danielson 2012). The anomalously "warm" year of 2016 coincided with an El Niño. In contrast, temperatures from throughout 2017 were generally within the typical range, suggesting a return to normal conditions. Although salinities in both 2016 and 2017 were lower than average in the upper 20 m, this could relate to higher than average precipitation or directly to an acceleration of snow and glacial melt during summer months. If the fresher-than-average waters of the bay were driven by accelerated melt, we might expect anomalous low salinity values to continue within the coming decades as a consequence of global warming. This could also lead to a decrease in nutrient concentrations in the euphotic zone surface due to increasing stratification and the low nutrient content of melt water. Were this to affect phytoplankton production, then zooplankton abundance would also decrease, lowering overall productivity in the ecosystem.

In summary, our findings indicated a depth pattern of zooplankton structure including prominence of *Acartia* and *Oithona* in the upper strata, *Metridia* in the lower strata, and *Pseudocalanus* throughout the water column in daylight hours. There was a pronounced seasonal

pattern of zooplankton in the upper water column (2-50 m) with greatest abundances and biomass in the spring-summer months of 2016 and 2017. *Metridia* genera accounted for the heaviest biomass in peak months compared to any other copepod, with the largest biomass visible in the lower strata during the day. Zooplankton concentrations within the bay are often an order of magnitude higher than outside. The Glacier Bay, Alaska, zooplankton community composition is similar to that of Icy Strait, British Columbia, GoA, and West Greenland except for the absence of two large-bodied copepod genera, *Calanus* and *Neocalanus*. We postulate that these genera are not significant due to reduced advection along the bay's shallow entrance sill and waters overall too shallow for these pelagic species to inhabit year-round.

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Appendix I. Zooplankton taxa abundance and biomass found in Glacier Bay, AK in 2016-2017. UC represents upper water column samples (0-50 m), LC represents lower water column samples (50-180 m).

Taxa or Species	Average Abundance UC (indiv. m^{-3})	Average Abundance LC (indiv. m^{-3})	Average Biomass UC (mgm^{-3})	Average Biomass LC (mgm^{-3})	Frequency of Appearance in UC	Frequency of Appearance in LC
Acartia longiremis	369	50	1.39	0.19	80	46
Calanus (*C. marshallae* and *C. pacificus*)	4	5	0.48	0.91	52	46
Chiridius gracilis	1	4	0.05	0.16	5	11
Centropages abdominalis	7	6	0.08	0.18	23	31
Epilabidocera amphitrities	<1	<1	0	0.07	2	2
Eucalanus (E. bungii and E. elongata)	<1	<1	0.31	1.14	25	41
Gaetanus brevispinus	<1	<1	0.01	0.04	3	2
Heterorhabdus tanneri	2	1	0.69	0.03	4	4
Metridia (M. okhotensis and M. pacifica)	337	632	17.54	44.52	78	63
Microcalanus pygmaeus	6	33	0.01	0.05	29	52
Neocalanus (N. plumchrus, N. flemingeri, N. cristatus)	18	5	1.39	0.15	25	14
Candacia bipinnata	<1	6	0.01	0.14	5	8
Pseudocalanus (P. minutus, P. newmani, P. mimus)	3651	1271	11.31	6.55	84	63
Tortanus discaudatus	<1	<1	0.05	0	4	1
Oithona similis	891	280	1.1	0.34	84	63
Triconia borealis	222	123	0.29	0.19	71	62

Spinocalanus (S. horridus and S. longicornis)	0	<1	0	0.17	0	4
Corycaeus angelicus	<1	2	0	0.01	10	12
Harpacticoida	6	2	0.02	0	36	25
Copepod nauplii (Harpactocoid, Calanoid, Cyclopoid)	737	103	0.53	0.08	84	62
Ostracoda	21	81	0.03	0.14	44	47
Oikopleura (O. labradoriensis and O. vanhoeffeni)	88	40	4.19	0.06	62	36
Fritillaria borealis	2	0	0.05	0	4	0
Limacina helicina	101	15	0.42	0.1	60	40
Clione limacina	<1	<1	0.07	0.1	4	7
Chaetognatha	22	4	6.34	2.9	77	61
Parasagitta elegans	<1	0	0.02	0	4	0
Podonidae	<1	0	0	0	3	0
Euphasiacia	25	12	0.26	0.25	36	24
Mysidae	4	2	1.28	5.22	27	26
Hippolytidae	<1	<1	0.02	0.01	7	2
Thysanoessa (T. inermis, T. longipes, T. raschii)	<1	<1	0.19	0.01	6	4
Bivalve larvae	591	46	0.19	0.02	61	32
Cirripedia	132	33	0.94	0.45	60	32
Themisto (T. pacifica and T. libellula)	<1	<1	0.04	0.16	12	5
Hyperoche	1	<1	0.11	0.17	9	10
Primno macropa	<1	<1	0.04	0.04	2	4
Gammaridae	<1	0	0.17	0	7	0
Hyperia	2	<1	0.14	0.13	18	24
Cyphocaris challengeri	2	6	0.68	1.81	43	50

Isopoda	3	2	0	0	23	23
Dimophyes arctica	<1	0	0.28	0	4	0
Decapoda	1	<1	0.05	0.09	19	8
Paguridae	<1	<1	0	0	5	1
Annelida	<1	<1	0	0	4	6
Medusozoa	<1	2	0.03	2.95	15	19
Polychaeta	41	20	0.21	0.12	36	26
Fish larvae	<1	<1	0.07	0.04	4	4
Ophiuroidea	66	17	0.02	0.01	30	22
Mertensia ovum	5	0	0.49	0	2	0
Echinodermata	1	0	0.19	0	2	0
Aglantha	<1	0	0	0	2	0
Megalops	<1	0	0	0	1	0
Scaphocalanus acrocephalus	<1	0	0.04	0	1	0
Haloptilus	<1	<1	0.04	0	1	1
Aetideus minutus	0	<1	0	0.01	0	1
Beroe	0	<1	0	0.01	0	1

Appendix II. Months sampled physical, chemical, and biological parameters for this study in Glacier Bay, AK.

Parameters labelled: DO (dissolved oxygen), S (salinity and density), PAR (photosynthetically active radiation), Fl (fluorescence), NO_{3-} (Nitrate), PO_4^{3-} (Phosphate), $Si(OH)_4$ (Silicate), NH_4^+ (Ammonium), TA (total alkalinity), DIC (dissolved inorganic carbon), pH, pCO_2 (partial pressure of carbon dioxide), Ω_{Ca} (calcium saturation), Ω_{Ar} (aragonite saturation), Chl (chlorophyll-a), UC (upper water column (0-50 m) sampled for zooplankton), LC (lower water column (50-180 m) sampled for zooplankton).

	Parameters sampled and calculated for 2016-2017 study duration (additionally October 2015)												
		2015	2016						2017				
		Oct	Jan	Apr	May	Jul	Sep	Oct	Jan	Apr	May	Jul	Sep	Oct
Physical	DO	x	x	x	x	x	x	x	x	x	x	x	x	
	S	x	x	x	x	x	x	x	x	x	x	x	x	
	PAR	x	x	x	x	x	x	x	x	x	x	x	x	
	Fl	x	x	x	x	x	x	x	x	x	x	x	x	
Chemical	NO_3^-	x	x	x	x	x	x	x	x	x	x	x	x	
	PO_4^{3-}	x	x	x	x	x	x	x	x	x	x	x	x	
	$Si(OH)_4$	x	x	x	x	x	x	x	x	x	x	x	x	
	NH_4^+	x	x	x	x	x	x	x	x	x	x	x	x	
	TA	x	x	x	x	x	x	x	x	x	x	x	x	
	DIC	x	x	x	x	x	x	x	x	x	x	x	x	
	pH	x	x	x	x	x	x	x	x	x	x	x	x	
	pCO_2	x	x	x	x	x	x	x	x	x	x	x	x	
	Ω_{Ca}	x	x	x	x	x	x	x	x	x	x	x	x	
	ΩAr	x	x	x	x	x	x	x	x	x	x	x	x	
Biological	Chl	x	x	x	x	x	x	x	x	x	x	x	x	

	UC	x	x	x	x	x	x	x	x	x	x	x	x	x
	LC	x	x	x	x	x	x	x	x	x	x	x		x